MORPHOLOGY AND TAXONOMY OF INTERTIDAL DWARF-BUGS (HETEROPTERA : OMANIIDAE FAM. NOV.) *)

by

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Abstract

The present revision of *Omania* has resulted in the following classification: *Omania coleoptrata* Horváth 1915, *Corallocoris* (gen. nov.) *marksae* (Woodward 1958) (= *samoensis* (Kellen 1960) syn. nov.), *C. satoi* (Miyamoto 1963), *C. nauruensis* (Herring & Chapman 1967). *Omania* Horváth 1915 is raised to family rank (Omaniidae fam. nov.) on the basis of egg, larval, external and internal adult structures of the species reviewed. New distributional and habitat records, and a key are given. Characteristics described include the mouthparts, salivary pump, pharynx pump, metathoracic scent-gland, grasping structure of the male and genital organs. Data from other families are compared. The relationship of Omaniidae to other leptopodoid families is schematized in an evolutionary diagram.

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*) Dedicated to the Dutch hemipterist Dr. H. C. Blöte on the occasion of his 70th birthday.

INTRODUCTION

Omania species are minute (1.2—1.6 mm) and live secretively in the intertidal zone. Hence they have been rarely collected in the past. Only five species have been described: 1. *O. coleoptrata* Horváth 1915 (Oman Gulf and Red Sea), 2. *O. marksae* Woodward 1958 (NE Australia), 3. *O. samoensis* Kellen 1960 (Samoa, Polynesia), 4. *O. satoi* Miyamoto 1963 (Japan), 5. *O. nauruensis* Herring & Chapman 1967 (Nauru, Micronesia).

These tiny dark bugs superficially resemble Schizopteridae, but certainly have no phylogenetic relationship with them. Since the genus was erected, *Omania* has been placed in Saldidae. Arguments will be given below to establish it in a separate, though related family. Of the type species, *O. coleoptrata,* only two specimens were known. Through recent rediscovery of the species, material came available for dissection, enabling adequate comparisons with some of the later described species. As a result it seems necessary to consider *Omania* as a monobasic genus and to create a new generic name to accommodate the species other than *coleoptrata.* The taxonomic status of *O. marksae* and *samoensis* is discussed in view of newly discovered localities of the former.

I. TAXONOMY OF GENERA AND SPECIES

GENERA

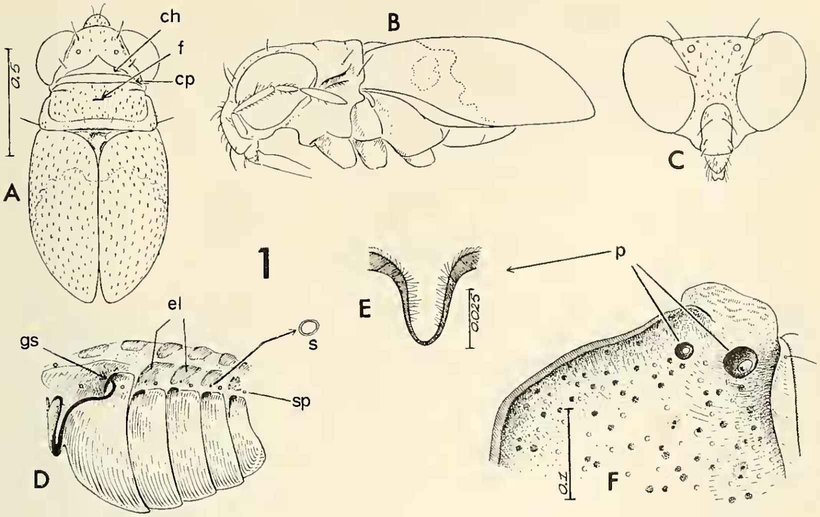
From the original descriptions it already seemed that the known species of *Omania* form two groups on the basis of external features. *O. coleoptrata* is separated from the other recorded species by the large, sharply triangular head collar and by the absence of any suture on the coriaceous fore wings. Scrutiny of other, specially internal structures of *O. coleoptrata* and *marksae* revealed a number of differences which set the two species more widely apart than initially thought. The discrepancies are even more striking than those which are often used as generic limits in other families, for instance Saldidae, Gerridae. Therefore it is proposed to establish a new genus, distinguished from *Omania* sensu stricto by the following diagnosis.

Corallocoris genus novum

Collum-like area of the head demarcated from the vertex by a broadly arcuate line (Fig. 6B). Fore wing with claval and R + M suture (Fig. 2G). Grasping structure of ♂ marked by a deep laterotergal cleft in the third abdominal segment, which fits against a pleural projection of the preceding segment (Fig. 2 K-M). Ponticulus basalis of phallus without dorsal projection (Fig. 11 I).

Type species, *Omania marksae* Woodward.

Fig. 1 A-F: *Omania coleoptrata.* A-C: type specimen (♀) of *Dollfusella minutissima* (the Paris Museum); D: male abdomen, lateral, genital segments omitted; E: optical section through hemielytral pit; F: base of hemielytron, ventral. 2 A-O: *Corallocoris marksae,* paratype specimens. A: lateral view; B: ventral view of thorax, coxae and wing of left side omitted; C, D: pygophore, dorsal and lateral; E: rostrum; F: hind leg; G: base of hemielytron, ventral; H: abdomen of female, lateral; I: posterior view of pronotum; J: pronotum, obliquely lateral; K-M: base of male abdomen; K: lateral; L: ventral; M: dorsal; N: scutellum, ventral; O: head, front view. ch, cephalic collar; cp, pronotal collar; cx, coxa; el, external laterotergite; ep, episternum; f, fovea; gs, grasping structure; p, pit; s, sensillum; sp, spiracle



1

A
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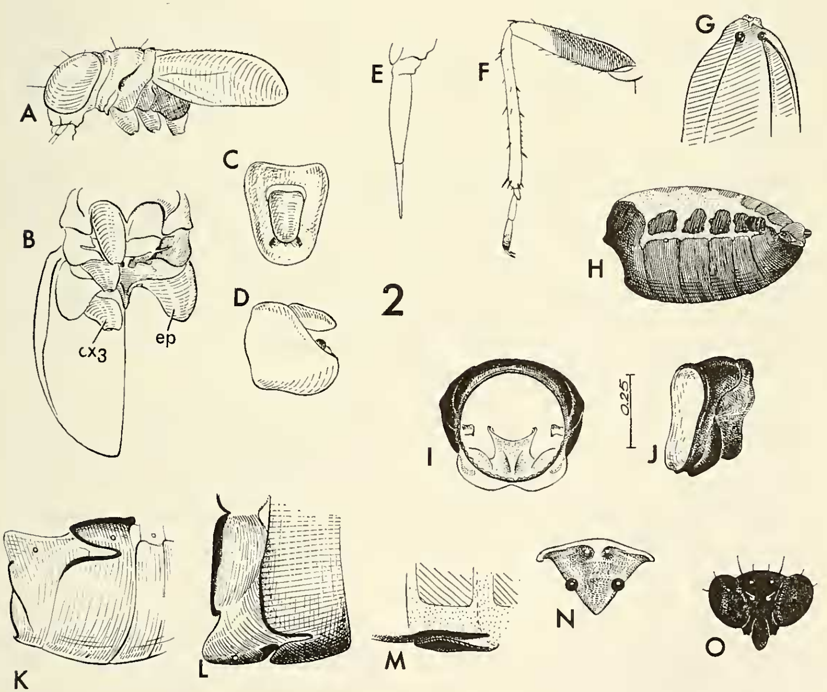

2

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K
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O

Omania Horváth, 1915

Collum-like area of the head demarcated from the vertex by a line which makes a sharp triangular incision anteromedially (Fig. 1A, 6A). Fore wing lacks claval and R + M suture. Grasping structure ♂ rather simple (Fig. 1D). Ponticulus basalis of phallus with a dorsal bridge-like projection (Fig. 12 C, E).

Type species, *Omania coleoptrata* Horváth, 1915.

Species

Omania coleoptrata Horváth, 1915

Horváth (1915) described the species from a single female specimen (Arabia: Muscat in Prov. Oman, May 1902, leg. L. Biró), which was deposited in the Hungarian Museum, Budapest. Unfortunately it could not be traced in that Museum and Dr. Soós assumed (litt. pers., 1958) that it must have been destroyed during the uprising in 1956. Drake (1961) has given a short note on the distribution of *O. coleoptrata* referring to his own collection material. The Drake Collection is now in the Smithsonian Institution, so I wrote to Dr. Froeschner, Curator of the Division of Hemiptera of that Institution, asking him about locality records of the species Dr. Drake had mentioned. The locality data conformed precisely with those given by Horváth (1915) in his original description of the species. Dr. Froeschner wrote to me (April 1969): "Thanks to the information you supplied, I now feel confident that the specimen in the Drake Collection must, indeed, be the lone type specimen of Horváth. Drake and Horváth had a long correspondence with many exchanges and loans of specimens. Perhaps Drake concluded the specimen to be part of an exchange and not the type because he marked it 'paratype'. The type of *Omania coleoptrata* definitely belongs to the Hungarian Museum and must be returned to it".

Through the kind cooperation of Dr. Froeschner (Washington) and of Dr. Soós (Budapest), I had the opportunity to study the Horváth specimen on its way to its legitimate location. It proved to be a male, and not a female. Measurements of this holotype are given in Table I (spec. a). The hairs of the specimen are largely rubbed off, legs and antennae are concealed by the glue, the left fore and hind leg, as well as all tarsal segments are broken off. Because of the rather poor condition of this unique specimen from Oman, the material from the Red Sea region to be mentioned below can only provisionally be considered as conspecific.

The second specimen known was described by China (1938) as *Dollfusella minutissima* (Egypt: Island of Sénafir at the southern extremity of the Sinai Peninsula, leg. R. Dollfus, 15.IV.1928). In 1943, Poisson & Poisson synonymized *D. minutissima* with *O. coleoptrata.* I restudied this single specimen in the Paris Museum. Despite the statement in the original description that it was a male, it proved to be a female. In addition to the excellent general figure presented by China, some external details of this specimen are given (Fig. 1 A-C).

Recently, the species was rediscovered and collected in moderate numbers by Linnavuori (3.X.1962, Red Sea coast, 50 km N. of Mersa Alam, Egypt; see Linnavuori, 1964) and by Riedle & Kirstener (1961/62, Al-Ghardaqa, Egypt; see Schuster, 1965). Data of some specimens are given in a list with measurements (Table I spec. b-e) and in the illustrations (Fig. 1 A-F, 3, 6A, 12). The differences from the other omaniid

Table I (measurements in mm)

Species	specimen	origin	head						pronotum		scutellum		antenna				leg 3		
			sex	total length	total width	width	vertex at level of ocelli	frons at narrowest width	length	width at the base	length	width	1	2	3	4	tibia	2ta	3ta
O. coleoptrata	a	holotype Oman	♂	1.38	0.64	0.52	0.22	0.13	0.27	0.52	0.15	0.25	0.1	0.19	0.13	0.23			
	b	Sénafir	♀	1.38	0.72	0.52	0.24	0.12	0.26	0.50			0.12	0.19	0.12	0.22			
	c	Al-Ghardaqa	♀	1.44	0.70	0.54	0.23	0.12	0.25	0.51			0.11	0.17	0.12	0.22	0.59	0.10	0.12
	d	N. of Mersa Alam	♂	1.38	0.60	0.53	0.23	0.11	0.25	0.48				0.17	0.11	0.21	0.54	0.08	0.11
	e	,,	♂	1.28	0.55	0.53	0.23	0.12	0.23	0.44				0.17	0.11	0.20			
O. marksae	f	Queensland	♀	1.58	0.80	0.60	0.25	0.11	0.30	0.59			0.12	0.18	0.16	0.23	0.60	0.08	0.11
	g	,,	♀	1.51	0.80	0.60	0.26	0.11	0.27	0.60	0.20	0.30	0.12	0.17	0.15	0.19	0.58	0.09	0.10
	h	,,	♀	1.53	0.80	0.60	0.23	0.10	0.26	0.58	0.20	0.30		0.18	0.15	0.18	0.62	0.12	0.10
	i	,,	♀	1.58	0.87	0.59	0.25	0.12	0.30	0.60	0.21	0.31		0.17	0.15	0.22			
	j	,,	♂	1.33	0.76	0.60	0.25	0.10	0.27	0.54	0.18	0.25		0.17	0.14	0.23	0.55		
	k	Samoa*	♀	1.59		0.62			0.26	0.59			0.12	0.16	0.14	0.23	0.58		
	l	,,*	♂	1.44		0.60			0.23	0.54			0.11	0.15	0.13	0.22	0.51		
	m	,,	♂	1.30	0.60	0.54	0.23	0.10	0.25	0.48	0.15	0.24		0.17	0.14	0.23	0.53	0.09	0.12
	n	Malaya	♀	1.48	0.77	0.59	0.25	0.11	0.25	0.56	0.20	0.32	0.10	0.18	0.12	0.20	0.55	0.10	0.09
	o	,,	♂	1.40	0.72	0.57	0.23	0.10	0.26	0.52	0.18	0.30	0.10	0.17	0.13	0.22	0.55	0.10	0.10
	p	,,	♂	1.15	0.57	0.53	0.20	0.08	0.25	0.45			0.10	0.15	0.12	0.19	0.48	0.08	0.08
	q	,,	♂	1.23	0.59	0.54	0.22	0.09	0.25	0.48			0.09	0.16	0.13	0.20	0.50	0.08	0.08
O. naurunensis	r	Nauru	♀	1.40	0.69	0.57	0.22	0.075	0.25	0.50	0.16	0.25	0.09	0.17	0.15	0.22			
	s	,,	♀	1.30	0.65	0.55	0.22	0.095	0.23	0.48	0.16	0.25	0.10	0.18	0.15	0.23	0.55	0.13	0.10
	t	,,	♂	1.21	0.60	0.55	0.22	0.08	0.23	0.48	0.18	0.21		0.19	0.14	0.23	0.55	0.10	0.10

* Average of five individuals, after Kellen (1960).

species are presented in the key on p. 69. The known distribution so far comprises only the Oman Gulf of the Indian Ocean and the Red Sea coast with certainty. The statement of Drake (1961, p. 303) that *O. coleoptrata* inhabits the seacoasts of the holomediterranean region must be an inaccurate interpretation of the literature. When asked to elucidate his information, the late Dr. Drake replied to Schuster (1965) that he had a specimen is his collection labelled mediterranean area'. On my request Dr. Froeschner checked the Drake Collection for *O. coleoptrata.* However, the type specimen from Oman, mentioned above, appeared to be the only representative. It seems therefore likely that Omaniidae do not occur along the Mediterranean coast, especially as Schuster (1965) failed to discover representatives in his inspections of the littoral fauna of the western and eastern coast of that region.

Corallocoris marksae (Woodward, 1958) and the identity of C. samoensis (Kellen, 1960)

Woodward (1958) described the species from a series of specimens from a northern and a southern locality in the Great Barrier Reef in Australia. New captures of the species show that it has a very wide distribution. I received from Dr. Carayon 3 ♀ collected by Mr. J. Plessis along the west coast of New Caledonia and 2 ♂ from Dr. C. H. Fernando, collected by Dr. D. H. Murphy along the seashore of the southern part of Singapore, Labrador Beach, Febr., 1961. A new rich locality was discovered by Dr. Murphy in Pulau Blakang Mati, Singapore (26.V.1969), where he collected about 60 specimens and 1 larva. These specimens were carefully compared with cotypes of *C. marksae* and no other conclusion could be drawn than that they are conspecific. In 1968 I suggested on the basis of external characters and of structure of the eggs, that *C. samoensis* could be synonymous with *C. marksae*. Kellen (1960, p. 496) summarized the differences from *C. marksae:* "the irregular light areas on the hemelytra are much bluer in *marksae* and more silvery in *samoensis;* the fine setae on the head of *marksae* are silvery, while in the present species they are golden; the second antennal segment of *marksae* is infuscated on the apical half [Woodward expressed this as follows: "apex of segment two brownish black", which need not to be the 'apical half', R.C.], while the same segment of the present species is entirely stramineous".

These are only minor colour differences. In many Saldidae such features vary between widely separated populations of one species. Moreover, I could not confirm the distinctions as constantly in combination, when studying paratypes of *marksae* and *samoensis.* Part of the collection from Singapore is intermediate between the Samoa and Australian specimens in the slight colour differences.

One could argue that prolonged disjunction of two populations of a non-flying insect would cause divergence in any case. Omaniidae are known so far only from the strongly semibrachypterous form (for terminology see Cobben, 1960) and hind wings are absent. Long-winged forms have never been found in intertidal saldids like *Aepophilus, Pentacora* and *Orthophrys.* In semibrachypterous species of *Salda* and *Halosalda,* macropterous animals are generally rare. The reduction of the fore wing in Omaniidae amounts to complete obscuration of the membrane and it is assumed that the present distribution of the species had already long existed. The initial conclusion that the populations from Samoa were morphologically conspecific with those of Australia (distance about 2700 km), suggests *C. marksae* to be a genetically highly stable species. The recent attributions from N. Caledonia (about 1400 km from the Great Barrier Reef in the

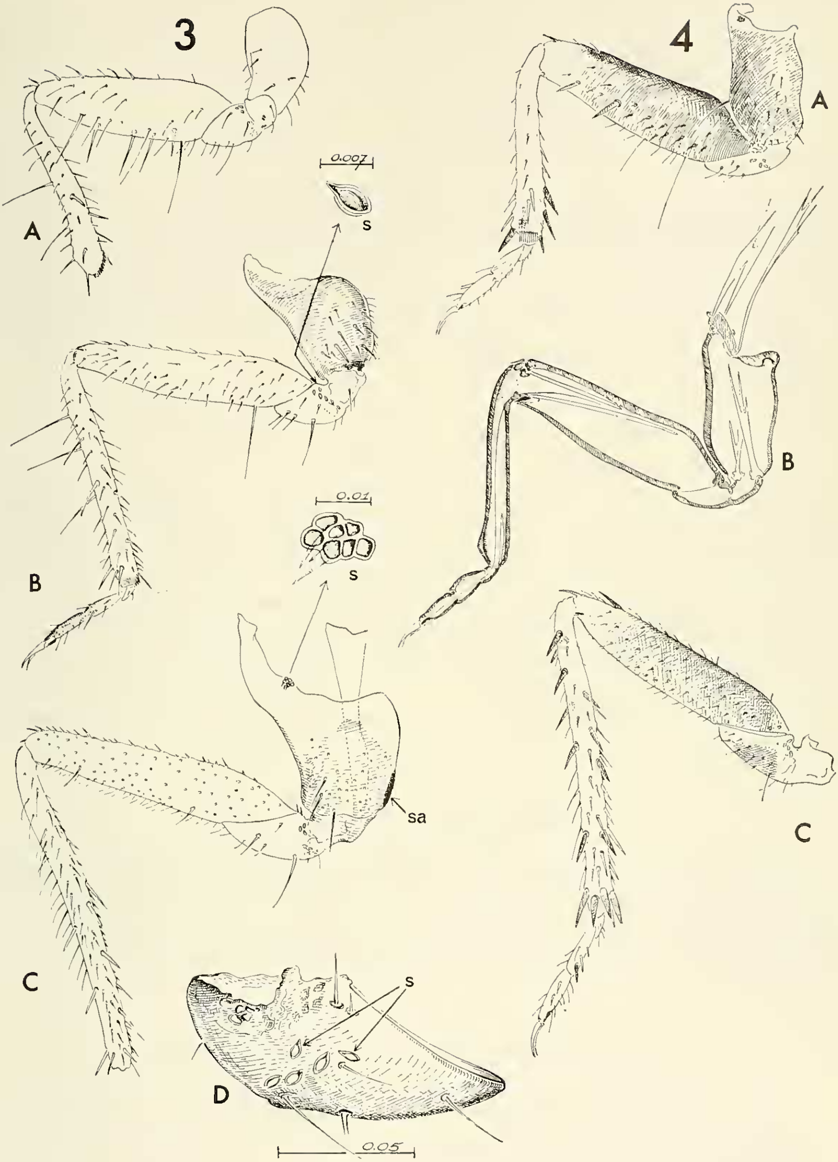

Fig. 3. A-C: *O. coleoptrata,* posterior view of adult legs; A, B, C: for, mid, hind leg, respectively; D: trochanter of larva V. 4. A-C: *C. marksae,* legs 1-3 of adult, aft aspect; B: mid leg showing articulation and tendons for muscle insertion. s, sensillum; sa, setose area

direction of Samoa) and from Singapore (about 4000 km in the opposite direction) confirms that we have here only one species. I herewith conclude to the following: *Corallocoris marksae* (Woodward 1958) = *C. samoensis* (Kellen 1969) syn. nov. The species will certainly be discovered along other coastal margins of the continent and islands in the Indian and Pacific Ocean.

The few, more or less intertidal Saldidae have a restricted distribution (*Aepophilus*, limited part of European Atlantic coast; *Orthophrys*, Atlantic coast of Morocco, Portugal; *Pentacora*, Mexican Gulf). These represent relic species of a more evolved family. As will be shown in section II, *Omania* and *Corallocoris* form a distinct clade group, away from the root of the Saldidae. Omaniidae, as denizens of a special ecological niche (survey on p. 71), for wich they are extremely well adapted by size, have probably remained evolutionarily static. In contrast to the numerous and genetically adaptable Saldidae, the few species of Omaniidae would not have had to compete with more advanced members of their own family.

Corallocoris nauruensis (Herring & Chapman, 1967)

This species from south-eastern Micronesia stands close to *C. marksae*. It is distinguished from the latter by the prunose coloration extending largely over pronotum and scutellum and by the slit-like median division of the pronotal dome. I could not confirm the morphometric differences given in the original description. The eyes of *C. nauruensis* are said to be proportionally longer and the scutellum smaller relative to other species. My measurements suggest no significant difference from other species. The posterior margin of the eye is said to extend beyond the posterior margin of the pronotal collar in *C. nauruensis*. In part of the series of *C. marksae* from Malaya it does, in another part it does not; this apparently depends on the angle of the head when the specimens are preserved.

Corallocoris satoi (Miyamota, 1963)

Omania satoi is placed here under *Corallocoris* on the basis of the shape of the head collar and the presence of two sutures on the forewing. These characters appear from the original description of the single female known. The generic assignment must be preliminary, until the two characters of the male, given in the generic diagnosis on p. 62, are checked.

KEY TO SPECIES BASED ON EXTERNAL CHARACTERS

Herring & Chapman (1967) presented a key to all the known species. They did not use the presence or absence of sutures in the hemielytra but stressed the relative size of the eye. In fact they start the key with this character which is difficult to assess for routine identification. Moreover, eye size is not distinctive between species. The species *coleoptrata, satoi, marksae* should have small eyes (width x 0.66 or less the width of the vertex at level of ocelli); *nauruensis* and *samoensis* should have large eyes (x 0.8 or more). Thus *marksae* and *samoensis* fall into different groups, but I have now synonymizid them. The character was checked in 4 paratypes of *samoensis* and in 5 of *marksae* and I found the indexes the same and with the same variation, viz. 0.65—0.8. The index varies in 4 specimens of *O. coleoptrata* from 0.6—0.67. The authors of the key give as first difference between *nauruensis* and *samoensis:* length of eye almost 1.5, as against no more than 1.25 length of pronotum, respectively. I found ratios of 1.35, 1.5 and 1.5 in specimens from Samoa and the averages of 5 individuals, given by Kellen, are 1.46 (♀) and 1.54 (♂).

A new key for the identification of Omaniidae is suggested here.

1. Collar of head sharply projecting medially into the vertex region (Fig. 6A). Ocelli not circular (Fig 6A). Forewing without sutures. Femora entirely stramineous (Red Sea, Gulf of Oman). . . . . *Omania coleoptrata* Horváth
— Collar of head with broadly arcuate anterior margin (Fig. 6B). Ocelli circular (Fig. 6B). Forewing with two longitudinal sutures (Fig. 2G). Femora dark with light apex 2
2. Bristle of head in front of bristle 1 (Fig. 6A); bristle 3 not arising from light spot. Fourth segment of antenna twice as long as third segment (Tokara Islands, Japan). . . . . *Corallocoris satoi* (Miyamoto)
— Bristles 1 and 2 of head in a straight line (Fig. 6B); bristle 3 arising from a light slightly elevated spot (Fig. 6B). Fourth segment of antenna 1.2—1.7 length of segment three. 3
3. Pronotum and scutellum black. Median fovea of pronotal dome is a simple pit (Samoa, New Caledonia, Australia, Malaya) . . *Corallocoris marksae* (Woodward)
— Pronotum and scutellum with light pattern. Median fovea of pronotal dome divides the dome posteriorly (Nauru Island, Micronesia). . . . . *Corallocoris nauruensis* (Herring & Chapman)

Beside the internal characters given in the generic diagnosis (p. 62, 64) and the external features given above, further differences of *O. coleoptrata* from *C. marksae* and *C. nauruensis* are: Dorsal hairiness somewhat denser and longer in *coleoptrata.* Bristles of head and pronotum brownish and more hair-like in *coleoptrata;* black, robust, more spiny in *marksae* and *nauruensis.* Cephalic bristle 3 on same level as the weak differentiation demarcating postclypeus from frons in *coleoptrata* (Fig. 6A), posterior of it in *marksae* (Fig. 6B) and *nauruensis.* Hemielytra more slender and uniform black, sometimes apical half with ashen gray bloom in *coleoptrata,* wider and with pruinose areas in *marksae* and *nauruensis.* Lateral hairs of tibiae longer than spines in *coleoptrata* (Fig. 3), shorter in *marksae* (Fig. 4) and *nauruensis,* which have more robust spines. Third abdominal spiracle of ♀ on pleural line in *coleoptrata,* below in *marksae* (Fig. 2H) and *nauruensis;* spiracles 4—7 on pleural membrane in *coleoptrata,* on laterotergites in *marksae* and *nauruensis.* When more material of *C. satoi* has become available, it can be decided how far these secondary features can be considered generic characteristics.

Larvae

Woodward (1958) described and drew the larval instars II-V of *C. marksae.* Kellen (1960) illustrated instar I and V of *C. samoensis* which is, as shown above, identical with *C. marksae.* Larva V of *Omania coleoptrata* is now at hand (Red Sea coast, Egypt) and shown in Fig. 8C. Comparison with Fig. 8A (instar V of *C. marksae)*

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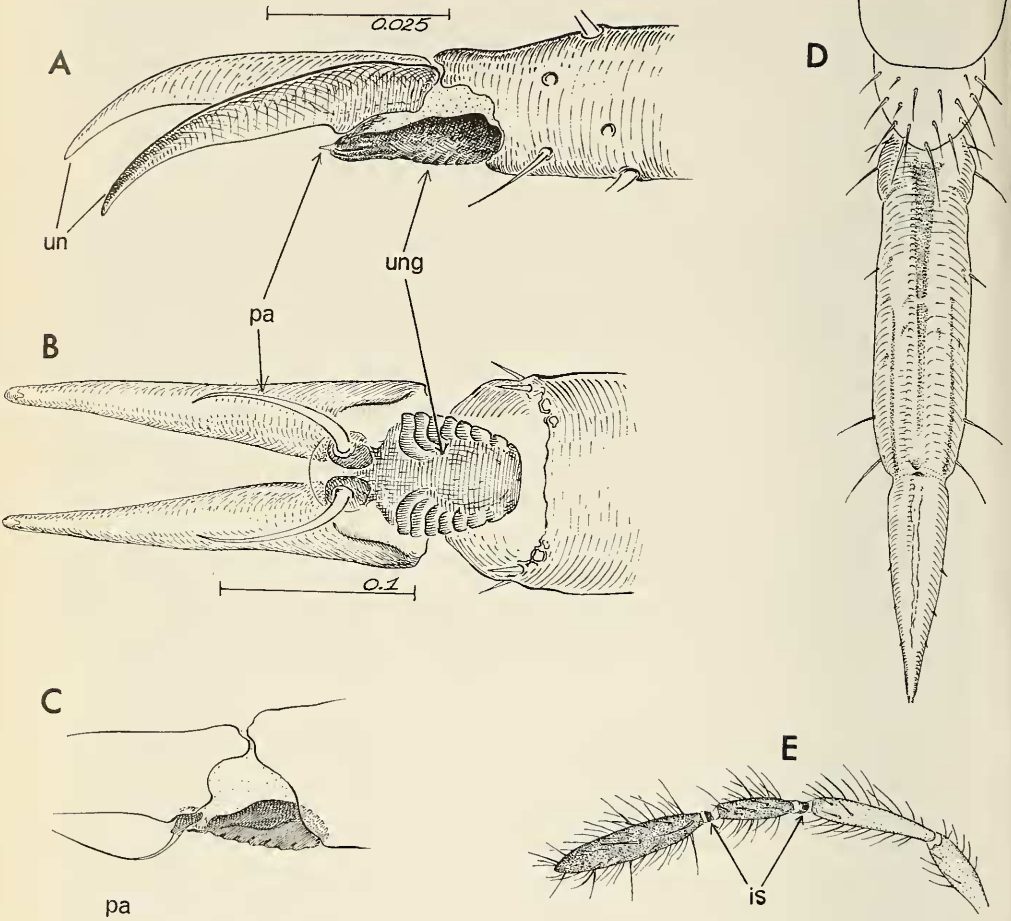

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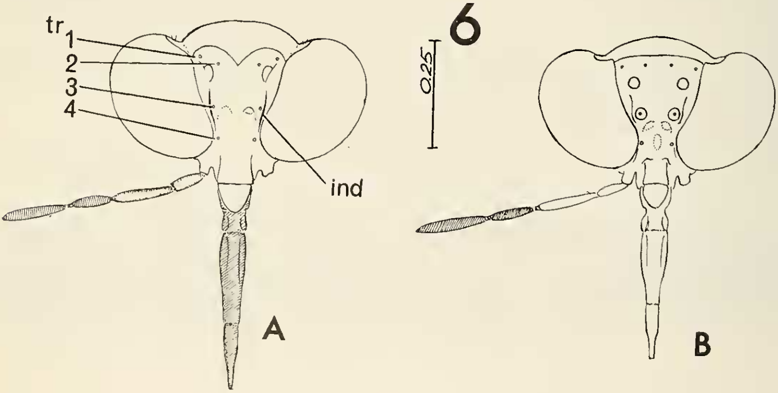

reveals discrepancies in number and arrangement of the primary hairs. These hairs form a distinct pattern on the abdomen, and *O. coleoptrata* has about half as many as *C. marksae*. However, small secondary hairs are more numerous in *O. coleoptrata*. This difference in chaetotaxy is generically significant. In Saldidae differences between genera are usually of a much lower order. Omaniid larvae lack a larval organ, which occurs in many Saldidae (Cobben 1957, 1959). The two adults of *C. marksae* from Singapore were accompanied by one small larva. A close study of this revealed a larval organ, so that I initially considered the omaniid adults to belong to a new taxon. Larval organs, however, always leave traces in the adults cuticle, as I have found in many Saldidae. Since the Singapore adults lack any spur of the organ, I conclude that the larva in question could not be omaniid, but is a saldid of unknown identity. A re-check of the chaetotaxy confirmed this conclusion. The second large sample of *C. marksae,* recently received from Singapore, contained one larva V which in fact lacked the larval organ.

Habitat

Omaniidae, for which I suggest the popular name 'intertidal dwarf- bugs' inhabit a particular ecological niche. They seem to occur always in a solid substrate with fine cavities to which the bugs can retreat during flooding by high tide. The substrate comprises coral rocks and pinnacles (Australia (32[1]), Red Sea (20), Micronesia (15), probably on Tokara Islands, Japan (22)), vulcanic rocks (Samoa (17)), and granite, Singapore (23). Schuster (1965) records *O. coleoptrata* from the foundations and loose rubble from walls of the old ruined building of the Marine Biological Station of Al-Ghardaqa, Egypt; the calcareous material originated from reefs nearby.

The bugs emerge from the crevices in a certain interval of time after the tide has receded. They are then found on the moist exposed edge and lower surface of the rocks and on the sand of rock beneath. The zones inhabited by Omaniidae seem to depend on the steepness of the intertidal shore area and the suitability of the crevices. Schuster mentioned that *O. coleoptrata* (Red Sea) occurred mainly just below the high tide mark. Kellen found *Corallocoris* only in those rocks lying in a narrow middle band of the intertidal zone; at high tide these rocks are covered up to two feet of water. He assumed that higher or lower rocks were either too dry or too wet for habitation. Dr. Murphy wrote to me that the habitat of *C. marksae* in Singapore: "is on very coarse sand and gravel at the base of vertical cliffs of granite at extreme high tide level — not as high as mean HW springs but not extending as low as HW neaps. Late on the day, small numbers extend up into the rocks but I believe most of the population is interstitial within the gravel".

A fine account of the biology of *Corallocoris* under laboratory conditions is presented by Kellen (1960). The relatively large eggs are glued to the substrate, deep in small holes and crevices in the rocks provided. The incubation period is about 16 days at about

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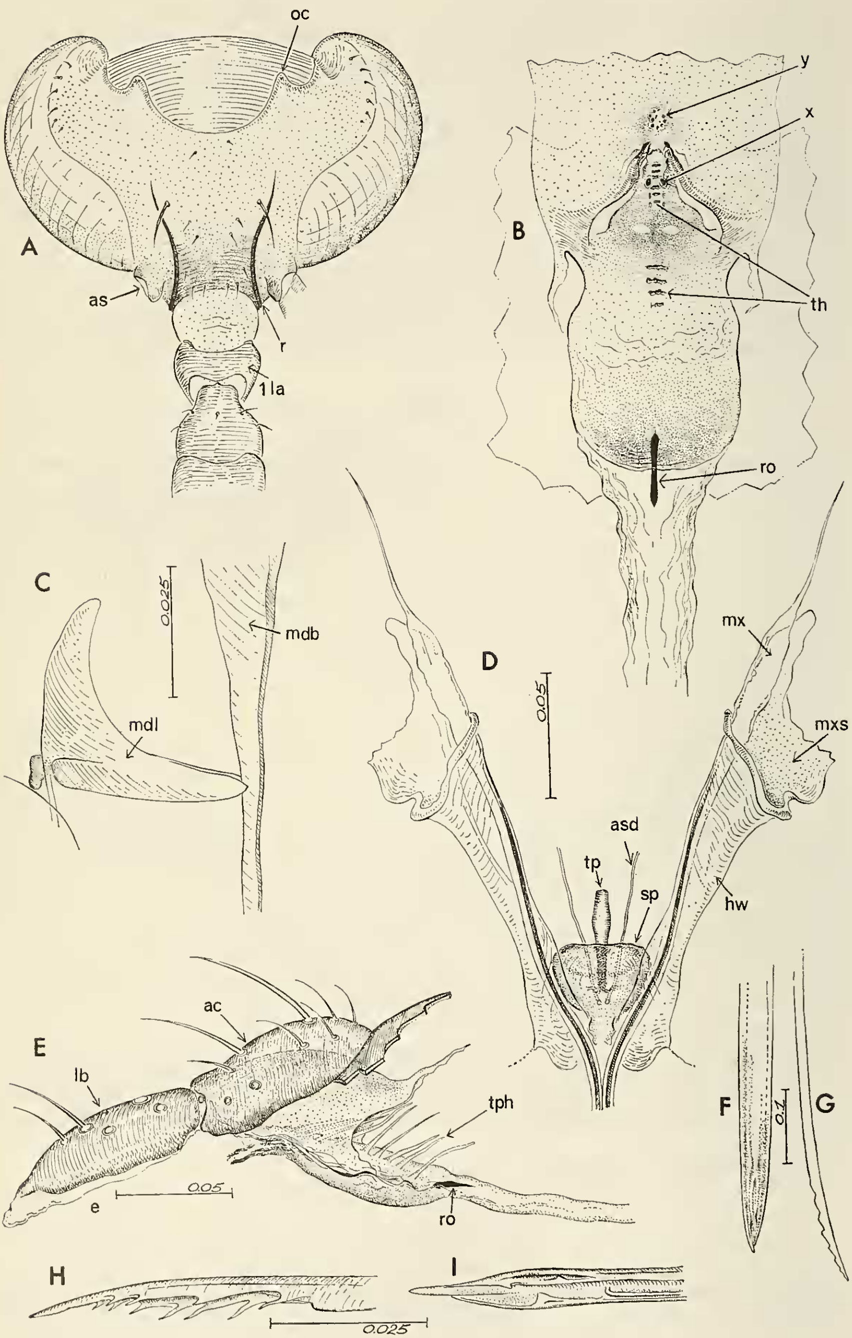
[1]) Numbers refer to literature list.

Fig. 5 A-E: *O. coleoptrata.* A: pretarsus of adult leg 2; B, C: pretarsus of leg 2 of larva V, ventral and lateral; D: rostrum of larva V, dorsal; E: antenna of adult. 6 A, B: frontal aspect of head, macerated; A: *O. coleoptrata;* B: *C. marksae.* ind, indentation of internal apodeme; is, internodial segments; o, ocellus; pa, parempodium; tr, trichobothrium; un, uncinus; ung, unguitractor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25° C. Larval development takes about a month. The adults can jump far. In nature, they prefer, when the tide is right, to run from one small hole or crevice to the next, investigating the surface of the rocks and small growths of algae with their beaks. Like all other representatives of the superfamily, Omaniidae are carnivorous. Kellen succeeded in rearing whole generations confining the animals to small stender dishes with pieces of rock and wet algae from the natural habitat. In captivity they seemed to feed on the organisms present in the algae, and on small psychodid and tendipedid larvae added to the dishes. Whether they prefer a particular prey in nature, is unknown. Woodward (1958) found the following fauna associated with *C. marksae:* Collembola, mites *(Microtrombidium* sp. and *Eupodes* sp.) and small beetles. The pieces of rock with *O.coleoptrata,* investigated by Schuster (1965), contained a very small species (0.8 mm) of Ptiliidae (Coleoptera) and numerous *Halophiloscia* sp. (Isopoda). The only other Heteroptera collected in the same habitat are *Halovelia* sp. in Australia (32), *Halovelia marianarum* Usinger in Micronesia (15), and a saldid larva in Singapore.

II. MORPHOLOGY, TAXONOMIC RANK AND PHYLOGENY OF THE GROUP

On the basis of head and male genital structures, it is postulated here that *Omania* and *Corallocoris* belong to the superfamily Leptopodoidea. Until now this group has consisted of the families Leptopodidae, Leotichiidae and Saldidae (including *Omania).* Discussions are largely limited here to conditions pertaining in Leptopodoidea in order to justify the establishment of the new family Omaniidae.

Egg

The egg of *C. marksae* is illustrated by Kellen (1960, his *O. samoensis).* He assumed from its large size relative to the female, that only one egg is laid every few days. I have reasoned earlier (1968, p. 372) that such a way of reproduction is suggestive of plesiomorphy. The number of ovarioles is not known but is probably less than 7, the normal number in Saldidae, except in *Aepophilus* which has 5.

Shape and sculpture of the omaniid egg superficially resembles that of remote families, e.g. Helotrephidae, some Notonectidae, Naucoridae or Schizopteridae. With even more families the omaniid egg shares the presence of only one micropyle. However the structure of the micropyle confines the omaniid egg definitely to the Leptopodoidea (Cobben 1968, p, 42). The shell of *Corallocoris* bears large hexagons, but the architecture looks light-optically solid, without any system of porosity for trapping atmospheric air. A completely solid chorion has been confirmed by electron-microscopy in another intertidal shore bug, *Aepophilus.* All other Leptopodoidea investigated, of which some also live close to the intertidal zone, possess aeropyles (Cobben *o.c.).*

Fig. 7 A-E: *O. coleoptrata,* larva V. A: head, ventral; B: pharynx pump, ventral; C: base of mandible with lever; D: base of maxillae, salivary pump, dorsal; E: pharynx pump, lateral. F-I: *C. marksae,* adult, distal part of stylets; F: maxillar bundle; G: mandible; H: right maxilla, lateral; I, left maxilla, inner view. ac, anteclypeus; as, antennal socket; asd, afferent salivary duct; hw, hypopharyngeal wing; la 1, first labial segment; lb, labrum; mdb, base of mandible; mdl, mandibular lever; mx, maxilla; oc, occipital condyle; r, ridge; ro, rod; sp, salivary pump; th, thickenings; tp, tendon of piston; tph, tendons of pharynx; X, Y, anterior and posterior sense organs

Larva

In contrast to egg and adult characters, larval characters are extremely difficult for delimitations above family rank. The first larval instar of representatives of various families were studied, in order to trace the significance of the primary setal pattern. The first instar of Saldidae (data from 15 species, 5 genera, 3 subfamilies) and Leptopodidae (1 species) share a similar hair pattern on the thorax, not encountered in other families; the pronotum (exclusive of lateral margins) bears four setae, the mesonotum and metanotum each bear two. The condition in Omaniidae does not conform to this. According to the careful drawing of the first instar of *C. marksae* (= *samoensis)* by Kellen, copied here in Fig. 8 B, the pronotum bears six and the mesonotum and metanotum each four setae. Saldidae and Leptopodidae have four longitudinal rows of setae on the abdominal tergum, but *Corallocoris* has six rows. Omaniidae, as represented by *Corallocoris,* share with Leptopodidae four vertex setae, but Saldidae (including *Aepophilus)* have more than four.

The most distinctive character of Omaniidae, separating them from related and, in fact, from all other families so far inspected, is the hair pattern of the compound eye. Omaniid larvae bear three distinct bristles inserted on the multi-faceted eye. The drawing by Kellen of the first instar shows only two bristles, but in the instars II-V, Woodward has consistently depicted three bristles. This larval character is retained in the adult and appears to be present in all Omaniidae studied. Judging from the condition of the eye bristles in the first instar and their fate during subsequent instars in other families, the first omaniid instar probably must also have three bristles. The function of the eye-bristles is still obscure but in other families they are trichobothria-like and are presumably sensory. The original number occurring in various, even remote, families, is two. This number occurs in all Saldidae studied and also in the first instar of *Leptopus* where they are transformed into pegs. Other characters of the omaniid larva, such as a single abdominal gland (between tergite 3 and 4) and presence of first abdominal spiracle are shared with other Leptopodoidea, but also with most Amphibicorisae. As said on p. 71, a larval organ typical of many Saldidae, is absent in Omaniidae. The eye of the young larvae is large, bearing numerous ommatidia, and the single abdominal gland is small. Both these facts place omaniid larvae on a higher anagenetic level than, for instance, Aepophilinae or Chiloxanthinae amongst Saldidae. Within the superfamily there is a progressive trend for increase of ommatidia and reduction of larval gland.

Adult

China (1933) has given a table with characters separating the families Saldidae, Leptopodidae and Leotichiidae, when creating the last family to include the two cave-dwelling species of *Leotichius.* Apart from the structure of the wings (no nervature left in Omaniidae), nearly all of the 11 characters listed unite Omaniidae with the Saldidae. The structures compared by China were predominantly external features such as characteristics of head, eyes, ocelli, clypeus, rostrum, antennae, pronotum, scutellum and legs. As will be shown below, there is only superficial resemblance between the two groups of shore bugs.

Head

Parsons (1962) has published a detailed study of the cephalic structures in one representative of the Leptopodoidea, *Saldula pallipes.* The terminology of her study and my own unpublished data on a wide variety of species are taken as background for the following review.

External

Omaniidae share with the Saldidae (inclusive of Aepophilinae) and Leptopodidae an internal dorsal apodeme, left and right in the frontal region (Fig. 8 D, E; ia). It lies close to the middle pair of trichobothria and is externally visible as a groove (Fig. 6A: ind). Structures of antennae (internodial pieces between segment 2—3 and 3—4) and rostrum (third segment longest) correspond with Saldidae.

The facial aspect of the omaniid head (Fig. 6) reveals some exclusive properties not found in Saldidae: a distinct collar-like vertex region, the presence of an extra pair of trichobothria-like bristles1) posterior to the ocelli, three trichobothria1) on the eye, no genal suture between mandibular and maxillary plates (also absent in *Aepophilus).* Unlike *Saldula pallipes,* there is no delimitation of mandibular plates and transverse swelling above the anteclypeus. But in Saldidae such boundaries arise with higher anagenetic levelling in the sequence Aepophilinae-Chiloxanthinae-Saldinae. In macerated preparations of Omaniidae, there are weak differentiations between the middle and anterior trichobothria (Fig. 6). These could represent the boundary between postclypeus and frons. The epipharynx protrudes only slightly ahead of the labrum, as in more primitive Saldidae. It does not project in *S. pallipes* and in other more evolved species of Saldidae. The gular region of the omaniid larva shows two longitudinal ridges passing ventrally to the antennal socket (Fig. 7 A; r). In *Saldula pallipes* and other Saldidae, a similar pathway is traced only by a faint line.

Internal

Pharynx

Fig. 7 B and E show the food pump so far as it is lined with cuticle. Its roof bears a longitudinal comb of about 10 tendons for the insertion of dilator muscles. Internally, the pump contains a median rod-like structure in the transitional zone where the pharynx narrows distally into the gut. The ventral wall of the epipharynx has a sensory plate just in front of the pharynx entrance. The plate is apparently a composition of about 10 spherical cells (y, Fig. 7 B). Posteriorly to this plate, thus as part of the food pump proper, lie two other imprints of supposed sensory cells (x). Further, mainly transverse differentiations (th), probably simple thickenings of the cuticle, are seen in this and other regions.

Omaniidae has the dorsal row of tendons in common with Leptopodoidea and, in fact, most other heteropterous families. In *Pentacora mexicana* there are 15 tendons, in*Chiloxanthus* 20, in *Aepophilus* 30 and in a leptopodid (*Valleriola* sp.) 23. Comparatively, the

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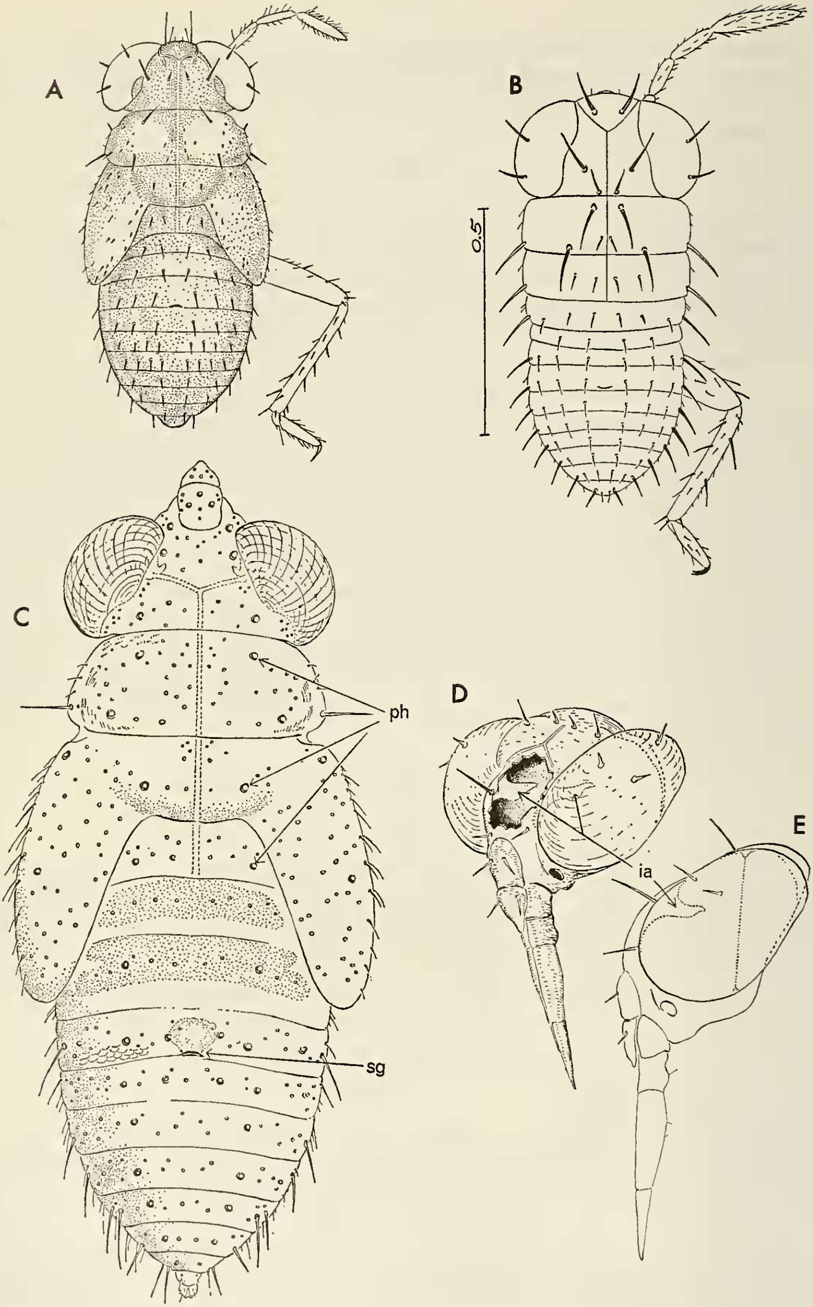
1) Although there is not yet histological or experimental proof that these setae are sensory, they are called here trichobothria for convenience. They are indeed homologous with the setae of *Aepophilus* and, for example, in most Amphibicorisae, where type of hair and insertion strongly suggest a particular function.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number in Omaniidae (10) is thus few; increase in tendon numbers could have some anagenetic meaning. Their presence excludes Leptopodoidea from typical Amphibicorisae. The type of dilator muscle insertion, direct or indirect, is an important factor for the evaluation of foodpump characters. However, in none of the recent surveys on the skeletomusculature of the heteropteran head including data on Amphibicorisae, I have found pharyngeal tendons expressely mentioned as absent. In accordance with other set of characters of Amphibicorisae (10, p. 363-378) I consider the lack of tendons plesiomorphic. The structure of the food pump in typical Amphibicorisae is trough-shaped and needs thorough histological investigation to compare it with the better known types of other families. Among Amphibicorisae there is one exception for Mesoveliidae, which from other evidence are grouped among aberrant water striders. *Mesovelia* has the mid-dorsal roof of the pump elevated, which bears a comb of 12 short tendons. A preliminary check in other family groups proved also absence of tendons in subfamilies of Reduviidae checked (Emesinae, Triatominae and Harpactorinae) and contrasts this group to Hydrocorisae, which indeed have tendons (Parsons 1966a, studied all hydrocorisan families except the extremely important Potamocorinae, which I consider to be a family). Other terrestrial families studied (inclusive of Dipsocoridae) have a distinct system of tendons, except two: Enicocephalidae and Pachynomidae. Of the former I studied one species of *Oncylocotis* which has an elongate food pump with about 25 very short tendons. Of Pachynomidae, a representative of each of the two subfamilies was examined: *Aphelonotus* had no tendons and *Pachynomus* sp. had 17 short tendons.

The distinct rod-like structure at the outlet of the food pump seems typical for Omaniidae; it could not be traced in Saldidae and Leptopodidae, or any other of the many families studied. Only in the saldid *Chiloxanthus pilosus* was a very faint strip visible in the same area.

The x-organ in *S. pallipes* is described by Parsons (1962) as an oval depressed area surrounded by a ridge. According to her: "Similar structures have been observed on the epipharynx of *Dysdercus* ("gustatory organ" of Macgill (1947)), *Gelastocoris* ("oval raised area" of Parsons (1959)), and *Gerris,* ("epipharyngeal sense organ" of Cranston and Sprague (1961)). They are probably sensory in function."

Parsons (1966 a) mentioned the organ for representatives of all hydrocorisan families and she described the nerve connexions. Of terrestrial Heteroptera, an accurate anatomical account is given for *Lygus pabulinus* (Awati, 1914) and *Triatoma* (Barth, 1952). A preliminary survey revealed that this epipharyngeal organ is generally present in Heteroptera, with some variations in cuticular appearance. In the saldid genera *Aepophilus, Chiloxanthus* and *Salda* it is an undifferentiated oval depression as in *Saldula pallipes.* In the primitive *Pentacora mexicana* the smoothly lined oval plate contains 9 circles each with a central point. In the leptopodid *Valleriola* sp. there are 12 of such circles. In Omaniidae the plate with 10 sensillae has an irregular outline. The anterior organ in Amphibicorisae is very much like in Leptopodoidea with a similar range of variation, as also in *Pachycoleus* and the pachynomid *Aphelonotus* sp. In families of

Fig. 8 A-E: larval structures. A-B, D: *C. marksae;* A: instar V; B: instar I (redrawn from Kellen 1960); C: *O. coleoptrata,* instar V, somewhat swollen in lactic acid; D, E: head of instar V; D: dorsolateral view, frontal exoskeleton cut away to reveal internal apodemes; E: as D, lateral. ia, internal apodeme; ph, implantation of primary hairs; sg, scent gland

other major groups there is much more differentiation towards distinct patterns of sensillae but there is no oval depression.

The variation in the posterior pharyngeal sense organs is greater. As shown above, in the one omaniid checked on this character, it is a single pair of oval 'cells'. Parsons (1962) did not mention them for *Saldula pallipes,* but species of *Pentacora, Chiloxanthus* and *Salda* possess two pairs, the most posterior differing in structure between the first two genera and the last. In some Amphibicorisae, I could not detect them, but in others there is one very faint pair, as also in the pachynomid *Aphelonotus* sp. In other families the number varies from two to four pairs, the latter condition being the usual.

Stylets and levers

Both mandibles are similar at their extreme tips; along the inner surface they are weakly notched with about seven indentations (Fig. 7 G). The lever is roughly triangular and one arm of it articulates directly with the stylet by means of its split tip (Fig. 7 C); the lateral corner of the lever forms the pivot in the cranium bordering the antennal socket.

The origin of the maxillary stylet (Fig. 7 D) extends as a fine thread from the maxillary sac. The latter structure envelopes the stylet as a spout-shaped membrane; it is wide open distally, at least in macerated preparations. The dorsal posterior margin of the sac is thickened and forms the structure which is probably homologous with the 'maxillary lever' in other groups. The morphology of the tips of the right (Fig. 7 H) and left (Fig. 7 I) maxillae are different, as in Saldidae. However, I could not detect in the left stylet the two rows of numerous fine spines which occur in Saldidae.

Structure of stylets and of levers relate Omaniidae more to Leptopodoidea than to Amphibicorisae. The latter have, as is known, a peculiar square mandibular lever whereas the maxillary lever is said to be absent in *Gerris, Velia* and *Hydrometra.* These two characteristics seem valid also for Hebridae, Mesoveliidae and aberrant genera I studied. Whereas the quadrangular type of mandibular lever separates adult Amphibicorisae (the lever in first larval instar of *Gerris* in fact is triangular!) from all other families of Heteroptera, the taxonomic value of the maxillary lever is difficult to assess. Parsons (1966 b) stressed that the distribution of the structure throughout the suborder is uncertain, since many authors overlooked it. Benwitz (1956) summarized literature data on groups of genera with a max. lever and those missing it, but certainly material should be rechecked. The constellation of the omaniid maxilla resembles that in the naucorid genus *Ambrysus* studied by *Parsons* (1966 b). She established the presence of a maxillary lever only in two of seven naucorid genera. She did not speculate on the evolutionary significance of the lever. From my own experience and from present knowledge of comparative morphology, I conclude that absence of maxillary lever is plesiomorphic. This should mean that the lever arose independently in different taxa along similar lines; the ultimate total structures arrived at are, however, quite varied by family group. A distinct lever is absent in Omaniidae, but present in Saldidae (including *Aepophilus)* and Leptopodidae. Besides Amphibicorisae, *Oncylocotis* (Henicocephalidae), some Hydrocorisae and apparently all Reduviidae lack a lever. The constellation of the maxillary sac in Reduviidae nevertheless reached great complexity in the more evolved taxa (e.g. Harpactorinae) as compared with the more primitive Emesinae. The Pachynomidae, a family of a vexing systematic position, have a lever like that of Nabidae and other

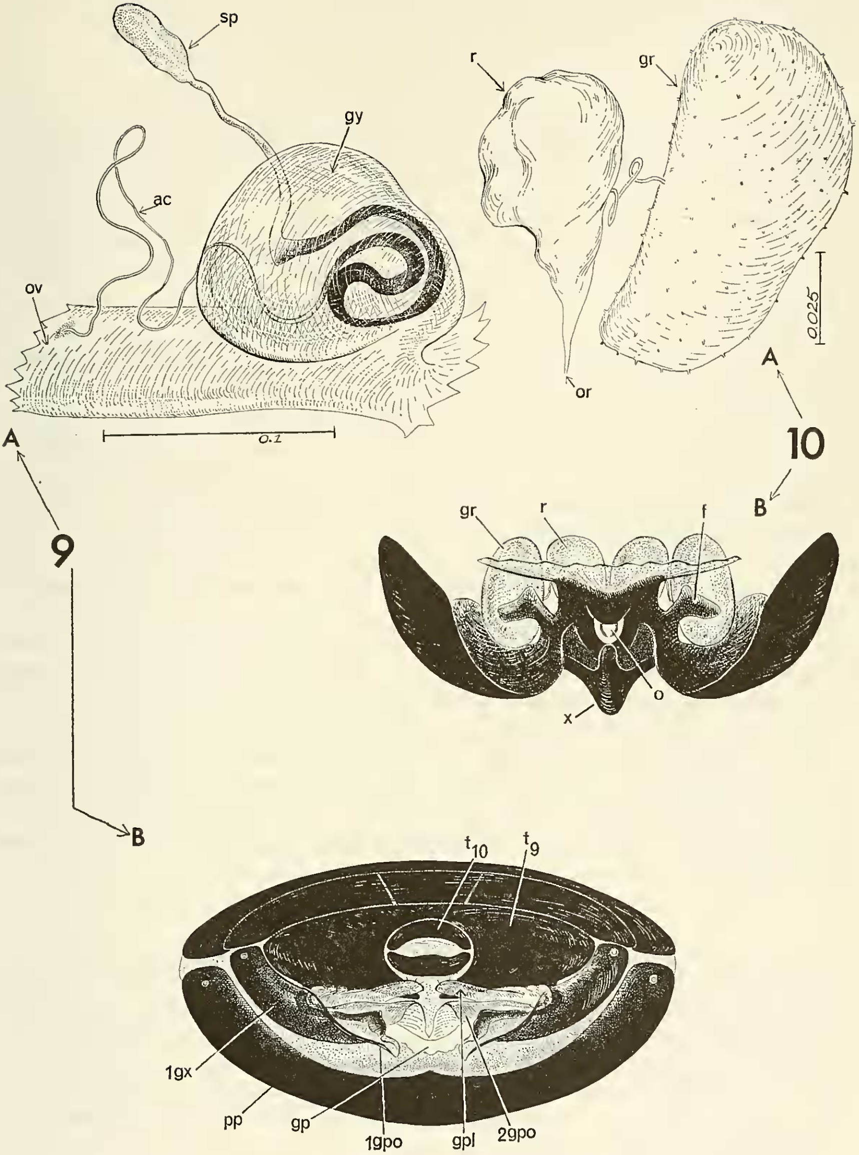


Fig. 9 A, B: *C. marksae,* ♀ genital structures. A: cuticular lining of genital tract; b, posterior view of abdomen. 10 A,B: metathoracal scent-apparatus; A: *O. coleoptrata,* gland and reservoir; B: *C. marksae,* entire glandular system, ventral part of metathorax from behind. ac, accessory canal; f, furca; gp, gonopore; gpl, gonoplac; gpo, gonapophysis; gr, glandular reservoir; gx, gonocoxa; gy, gynatrium; o, external outlet of scent glands; or, orifice of reservoir; ov, oviduct; pp, pregenital plate; r, reservoir; sp, spermatheca; t, tergite; x, xiphus

cimicoid groups. Species of all other groups, superficially checked, revealed a lever: Dipsocoridae, Thaumastocoridae, Pentatomoid families, Thaumastellidae (rather simple).

Salivary pump

Characteristics of the omaniid pump (Fig. 7 D, sp.) are: tendon of piston short, horizontally flattened; transverse circumference of posterior wall of pump chamber neatly circular; afferent ducts paired; efferent duct short.

Only these four outer aspects of the salivarium will be compared here with other families. Data from sections must wait later evaluation. The points to be discussed here throw some new light on modifications of the apparatus and its evolution: shape of pump chamber, orientation of piston tendon, whether afferent ducts have fused, length of efferent duct.

Like Saldidae and Leptopodidae the pump of the Omaniidae has the horizontally flattened piston tendon, the short efferent duct and paired outlet of the afferent ducts. The pump itself is, however, isoradial, whereas in *Valleriola* (Leptopodidae) and *Aepophilus* (Saldidae) the dorsal posterior wall is incised. This trend has progressed in other Saldidae so much that the dorsal wall became almost split along its median line. In Amphibicorisae, a cladistic trend is apparent in the Velliidae and Gerridae. There, the lateral sides of the chamber became inflected from behind. This trend is associated with shortening of the efferent duct. A long efferent duct is retained in other Amphibicorisan families, in Henicocephalidae *(Oncylocotis)* and in Emesinae *(Empicoris)* amongst Reduviidae. The afferent canals originally ended separately in the pump. Most Heteroptera and primitive Reduviidae are still like this. In the advanced reduviids the ducts anastomosed a very short distance terminally. In Miridae and Nabidae studied, there is a very long common afferent duct, a condition paralleled in Pachynomidae. In most Heteroptera the tendon of the piston is a vertical plate. As noted above, it is flattened in a horizontal plane in Leptopodoidea. So far I have encountered a horizontal tendon only in *Hebrovelia,* the gerrid *Trepobates,* the thaumastocorid *Xylastodoris* and the thaumastellid *Thaumastella.* In some Amphibicorisae and in *Oncylocotis,* the tendon is thread-like; it is assumed that this is the basal type from which flattening in one or the other plane arose.

Metathoracic scent-gland

The metathorax is characterized by a large shield-like epimeron which encloses the coxae laterally (contrast Saldidae, Leptopodidae). The adult scent-apparatus of Omaniidae is of a type encountered nowhere else in Heteroptera. Chlorazol preparations of *C. marksae* reveal four ovoid bodies in the metathoracic cavity and a single median ostiole for discharging the secretion (Fig. 10 B). The four reservoirs belong to a paired gland system, each side with two reservoirs united by a thin duct. The cuticular lining in *C. marksae* and in *O. coleoptrata* suggests that the most lateral reservoirs had a glandular layer all round. The cuticle projects out from the reservoir into short extensions, probably remnants of caniculi, regularly distributed over the whole surface of the voluminous reservoir. In ethanol-treated material, this reservoir is brownish yellow and its wall has a finger-print sculpture. The median bladder has an uninterrupted smooth wall and opens into the ostiole independently of the reservoir of the other side. Thus, the single external ostiole contains the outlets of the two reservoirs of the gland system, each outlet being governed by one dilator apodeme. From the condition of the system in other Leptopodoidea the glandular lateral reservoirs in Omaniidae are clearly homologous with the tubular gland system in other families. Saldidae except *Aepophilus* have one median reservoir and one ostiole. Leptopodidae have two reservoirs and two ostioles, in common with *Aepophilus*. However, *Leotichius* has one reservoir, but two ostioles. Thus, the situation in Omaniidae is peculiar in two respects: the doubling of the reservoirs with retention of the single external ostiole and the enormous widening of the gland ducts resulting in accessory reservoirs.

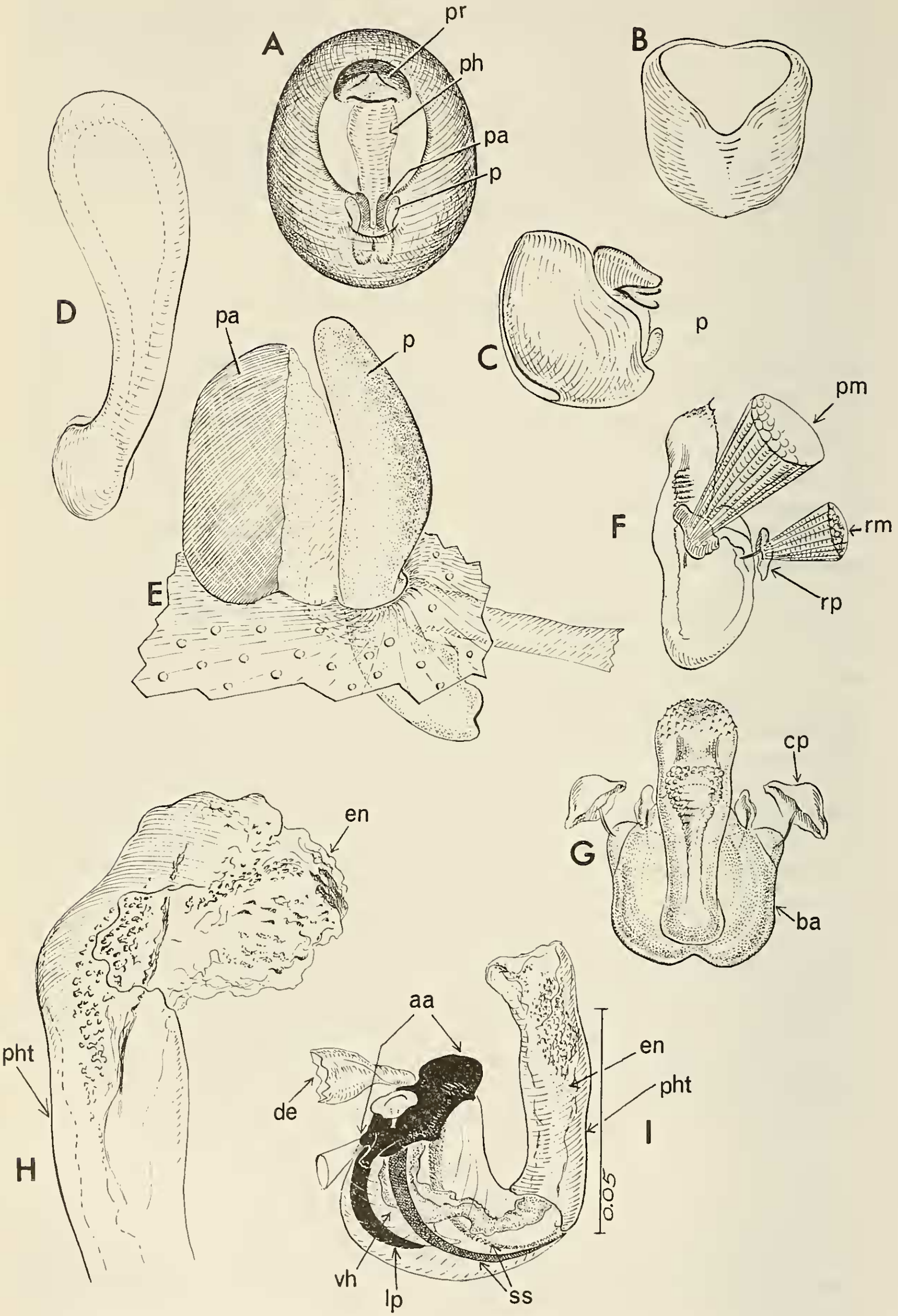
Legs

The hind legs of adult Omaniidae lack the terminal tibial comb and the two fragile curved setae on the ventral side of the first tarsal segment. Both these characters are features normal in Saldidae, the hind leg comb arising as a complete new adult structure. The simple pretarsal structures in Omaniidae are similar for all three pairs of legs and undergo a sudden reduction during adult moult. Besides the two claws there are only two parempodia, extensions of the unguitractor plate. In the last larval instar these parempodia are rather long curved spines (Fig. 5 B,C), but in the adult only small rudiments remain (Fig. 5 A, pa). Young instar larvae were not available. They ought to be studied to know whether traces of the arolia are present in the youngest stages. In typical Saldidae such traces are absent, but in the larvae of *Aepophilus* (not in adult!) one arolium occurs; I consider this homologous with the ventral arolium of Amphibicorisae, of which typical representatives possess a dorsal one too. Omaniidae share the abrupt reduction of the parempodia during one moult only with some saldids of the *Pentacora* group. In most Saldidae, the ontogenetic reduction of the parempodia proceeds gradually from the first larval instar onwards; the rate of reduction is sometimes unequal between the two parempodia of the same unguitractor plate. Other special structures of the omaniid legs occur widely in Heteroptera, even beyond. The third coxa bears a setose area at the inner side (Fig. 3C, sa). This is an adaptation to jumping; both rough spheres of the left and hind coxa are apparently pressed against each other during jumping. The structure occurs in the saltatorious Saldidae, Leptopodidae and also in Ochteridae. The trochanters are almost entirely subdivided by an internal cross-septum. One series of oval sensilla are arranged transversely on both lateral sides of all coxae (Fig. 3 B, D, s). These are probably stretch-receptors and occur in all heteropteran families studied so far. There are, however, differences in number, shape and arrangements of these organs, which must still be assessed for possible phylogenetic value. Another group of apparently sensory bodies occurs at the base of each coxa (Fig. 3 C, s). This cluster of conical projections is not restricted to Leptopodoidea. Omaniidae have no femoral plectrum nor a hemielytral stridulitrum, which are present in a number of Saldidae (joint work with J. Lattin).

Abdomen

Pregenital structures

The omaniid abdomen bears 8 pairs of spiracles as have all other Leptopodoidea and some other major groups (Cobben 1968, p. 377, 378). Their position, however, distinguishes Omaniidae from most Saldidae. In the former, the stigmata are situated in the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membrane between sternites and laterotergites (Fig. 1 D, 2 H). Most stigmata are enclosed in the connexival sclerites as in Leptopodidae. Trichobothria are absent but a campaniform sensilla occurs anterior to each mid-abdominal spiracle (Fig. 1 D, s). The stigmata of Saldidae lie ventrally at some distance from the lateral margin. In few species the spiracles have closely approached the ventral connexival borderline, but apparently never passed it. One could suggest that dorsal placement of spiracles could be related to respiratory adaptation in intertidal zones. Such a correlation is not apparent in Saldidae, of which some species are indeed intertidal. Even in *Aepophilus bonnairei,* pre-eminently an intertidal species, the spiracles are on the ventrites. Peculiarly, those saldid species in which the spiracles are more lateral, are found in several unrelated genera, and the distribution of those species is predominantly tropical. The spiracles in Leptopodidae, which are in general less hygrophilous than Saldidae, are dorsal on the external laterotergites.

The abdominal dorsum of Omaniidae is largely membranous, unlike in those Saldidae with shield-like hemielytra. The external laterotergites are distinct, but internal laterotergites, present in all Saldidae, are absent in Omaniidae as well as in Leptopodidae. The grasping structure in Omaniidae is quite different in constitution from that in Saldidae (including *Aepophilus).* This male apparatus formed by paratergites 2 and 3 was first described in Saldidae by Drake & Hottes (1951) as a stridulatory device, but Leston (1957) and Cobben (1957) showed that it serves to fix the male to the female hemielytron margin during copulation. In Saldidae grasping is as with a clip-type clothes-peg; friction is particularly caused by a transverse strip with pegs. As the structure increased in effectiveness, the female evolved a coadaptation in the wing area which is grasped. The coupling of male Omaniidae operates more like the paper-clips principle. There is no rough area to create friction. The laterotergite of segment 2 extends along the innerside of the modified laterotergite 3. The two adjacent lamellae (Fig. 2 K-M) apparently clip the female hemielytron. The latter has no special counterpart structure. Females, however, which have copulated or on which attempts at copulation have been made can be recognized as such. The male grasping structure scours the blue-grey wax of the female wing so that a shining black spot results, invariably close to the wing apex. Leptopodidae have the same characteristic side by side mating behaviour as Saldidae, and so do Omaniidae as deduced above on morphological grounds. But Leptopodidae have no structural adaptations; the female wing margin is simply pinched in the male pleuron between segment 2 and 3. This behaviour could have evoked pleural differentiations in Omaniidae, independent of Saldidae.

The pregenital glands, characteristic of all Saldidae, except *Aepophilus,* are absent in Omaniidae.

Genital structures

Female.

Internal ectodermalia (Fig. 9 A). The internal female organs so far as lined by cuticle,

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Fig. 11 A-I: *C. marksae,* ♂ genital structures. A: posterior view of pygophore; B, C: ventral and lateral view of pygophore; D: paramere; E: parandrium and dextral paramere; F-I: phallus; F, I: lateral; G: aft side; H: distal end of phallotheca, endosoma slightly extended, aa, articulatory apparatus; ba, basal aula; cp, capitate process; de, ductus ejaculatorius; ds, ductus seminis; en, endosoma; lp, ligamentous processes; p, paramere; pa, parandria; ph, phallus; pht, phallotheca; pm. protractor muscles; pr, proctiger; rm, retractor muscles; rp, retractor process; ss, sclerotized strip; vh, vertical hymen

are the same in three omaniid species studied. Of greatest interest is the full presence of a canal leading from the ventral side of the gynatrial sac forwards to enter in the roof of the common oviduct (Fig. 9 A, ac). Such a canal also occurs in most Amphibicorisae and has been termed 'fecundation canal' (Pendergrast 1957), by analogy with a similar duct in Carabidae. Scudder (1959) called it 'accessory canal' and this term is used here, as the function of the canal has not yet been established. Brinkhurst (1960), studying the gerrid *Aquarius najas,* had ideas about the homology and function of the canal with which I disagree and will discuss it elsewhere. In Omaniidae, the canal is very solid at the base and forms a spiral coil in the fold between gynatrium and oviduct. A median spermatheca is present (Fig. 9A, sp.), its short duct originating from the centre of the ventral wall of the gynatrium as a continuation of the accessory canal. The bulb is simple, irregularly shaped and without pump flanges. The gynatrium lacks thickened rudiments of a ringed gland. Compared with other Leptopodoidea, the omaniid condition with accessory canal and simple spermatheca is encountered only in Leotichiidae (Scudder 1959). What I consider to be rudiments of the accessory canal, exist in Leptopodidae; lining of a gynatrial ring gland is not visible in this family, but the spermatheca evolved in a firm structure with flanges. Besides a well developed spermatheca, a ringed gland clearly arose in Saldidae, and no trace remains of the secondary canal. But, the saldid *Aepophilus bonnairei* retained the plesiomorphic condition of the spermatheca: a wide cylindrical bulb with irregular transverse wrinkles, a short duct and absence of a cuticular flange for attachment of muscles. In other Saldidae, the spermathecal bulb is small, but stout, and with a proximal pump flange (except the primitive *Pentacora mexicana,* Lattin & Cobben, 1968). The spermathecal duct increased in length anagenetically as a longer phallic flagellum developed in the male.

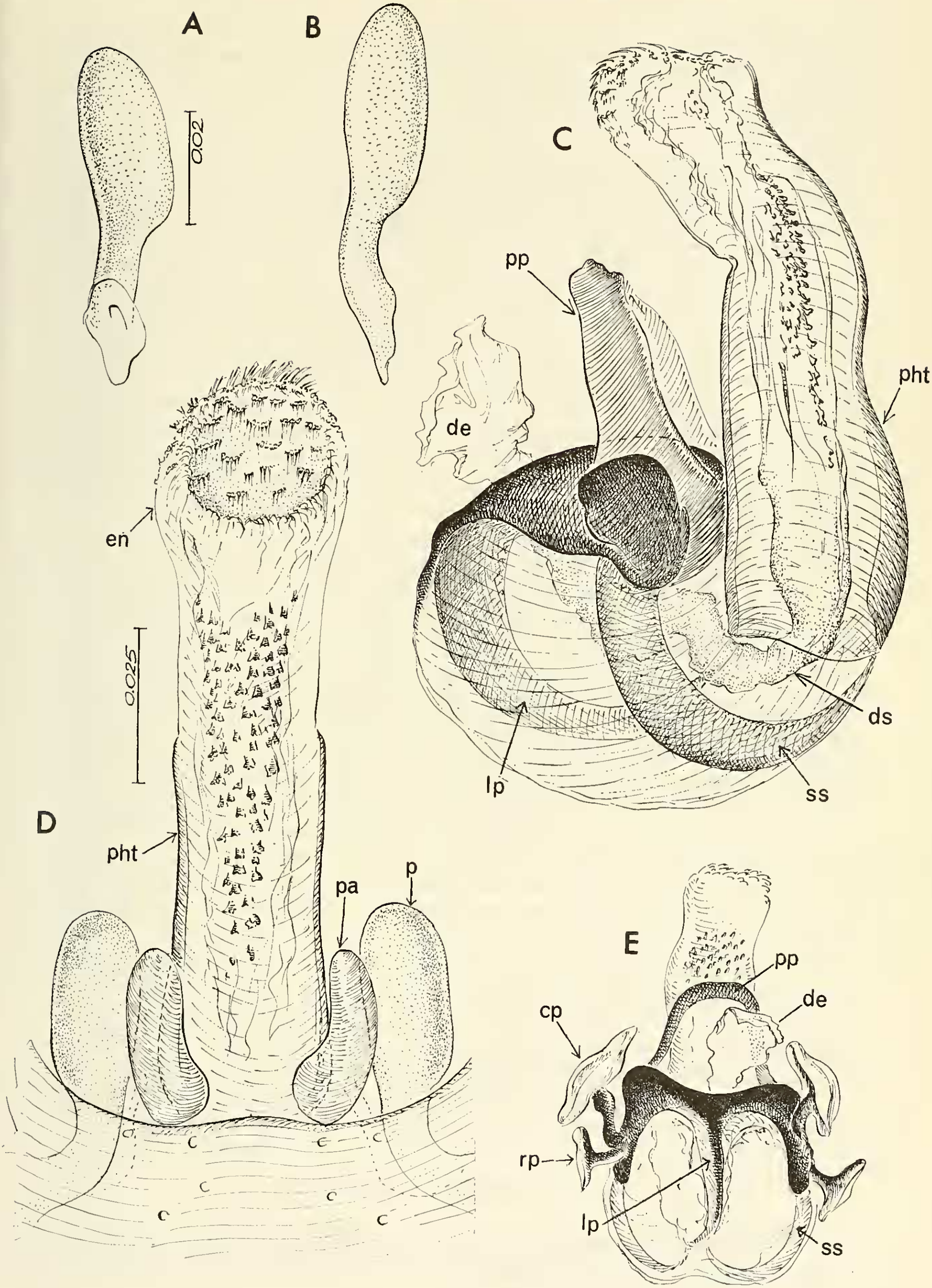
External ectodermalia (Fig. 9 B). — The apex of the abdomen is broadly rounded, sternite 7 shield-like, paratergite 9 not visible. The tergal part of segment 9 surrounds the proctiger as a very broad sheath. The proctiger is relatively large, with a well developed sternal part as in Amphibicorisae. Both pairs of gonapophyses (gpo) and the gonoplacs (gpl) are present, poorly developed, flap-like and lie in a transverse vertical plane. Only the second gonapophyses join each other along the median line. Because of the relatively large eggs, the gonopore is wide and clearly visible after staining with Chlorazol black (gp).

The vestigial terminalia distinguish Omaniidae from all Saldidae, including *Aepophilus,* which have a well developed ovipositor. None of the other Leptopodoidea have such plate-shaped genitalia as Omaniidae, and the situation in Leptopodidae and Leotichiidae is intermediate between this and the saldid type. The saldid condition is, in my view, apomorphic.

Male.

I presented a scheme of evolution of the leptopodoid phallus in 1965, for which representatives were chosen from Saldidae, Leptopodidae and Leotichiidae. A theory has been developed showing how the leptopodoid phallus could have evolved from the plesiomorphic condition as found in modern, typical Amphibicorisae. There was then

Fig. 12 A-E: *O. coleoptrata,* ♂ genital structures. A, B: right paramere, different aspects; C-E: phallus, endosoma slightly extruded; C: left lateral side; D: aft view; E: front view. pp, projection of ponticulus basalis. Further legend, as in Fig. 11


A
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no clear comparative picture of the omaniid phallus, because of its smallness and the scarcity of material for dissection. It will now be shown that the omaniid genital structures fit well into the basic leptopodoid plan, but that clade-characters strongly support family status.

The pygophore of Omaniidae is high and short (Fig. 11 A,C), with the aft side truncate and cleft medially. This cleft is formed by the interspace between the two vertical outgrowths of the capsule (Fig. 11 A,E, pa). Such projections are immobile and inflexible in Saldidae and have been named provisionally 'parandria', though they are recent structures and thus do not correspond to the original definition of the term. In Omaniidae, however, the parandria are demarcated from the capsule by a transverse suture, and they turn aside under tension of the adjacent phallus (Fig. 12 D, pa, tension by hot lactic acid). The minute, club-shaped parameres (Fig. 11 E, p) are encompassed by the wall of the capsule. This is also true in nearly all Saldidae and in Leotichiidae, but not in *Aepophilus* and Leptopodidae. The omaniid phallus proper has the following characters in common with other Leptopodoidea: basal articulatory apparatus with ponticulus basilaris and distinct promotor and remotor apodemes. Basal foramen with a septum that leaves uncovered a transverse slit round the ductus, allowing passage of haemocoelic erection fluid. Elongated, mutually fused ligamentous processes present. Ductus seminis very wide, flattened, attached medioventrally to basal apparatus and lengthwise with ligamentous processes by means of two vertical hymens. Basal aula spacious, membranous. Conjunctival part of endosoma not clearly defined.

All these characters do not apply to the amphibicorisan genitalia, which are in all ways much less evolved. Beyond the leptopodoid basic plan, each family has its own characteristics showing divergent phylogeny. Saldidae developed a highly complex internal reel-system, the rectilinear evolution of which could be solved stepwise. The ligamentous processes in Saldidae and Leotichiidae connect the basal apparatus with the ventro-basal edge of the phallotheca. In Omaniidae (Fig. 11 I, lp) and Leptopodidae, however, these processes extend only half way along the basal aula. Additional strengthening of structures associated with the basal aula arose in a different way for each family. The midventral edge of the phallotheca is in some Leptopodidae provided with a long projection to meet the distal end of the ligamentous processes. In others, the ductus seminis itself is cramped to the tip of the ligamentous processes. Strengthening of the hinge-point between phallotheca and basal aula developed in *Omania* along another path. A sclerotic strip runs in each lateral wall of the basal aula from the articulatory apparatus obliquely downwards to join the base of the phallotheca (Fig. 11 I, 12 C, ss). The phallotheca scarcely deserves this name in this family, as it is not sclerotic; its distal end is irregularly outlined laterally (Fig. 11 H). The endosoma could not be studied in inflated position. In retracted state it is a wide, wrinkled, membranous mass beset for much of its length with numerous groups of hooked spines (Fig. 12 D, en); sclerites are lacking. The intromittant organ in action must reach considerable length. Phallic structures are in their basal part more leptopodid-like, in their phallotheca-endosomal part more leotichiid-like. The organ is consequently remote from the saldid type.

Concluding remarks

The morphological survey has revealed many structural differences of the genera *Omania* and *Corallocoris* from other leptopodoid members. These discrepancies are

Table II

	Saldidae	Omaniidae	Leptopodidae	Leotichiidae
1. number of ovarioles	7 (rarely 5)	probably < 5	5	
2. egg deposition	mostly embedded	superficial	superficial	
3. chorionic aeropyles	mostly present	absent	present	
4. larval organ	mostly present	absent	absent	
5. primary metameric chaetotaxy of larva	4 : 2 : 4 pron. mes. abd.	6 : 4 : 6	4 : 2 : 4	
6. setae on head capsule	6	8	6	
7. setae on compound eye	2	3	2	
8. adult length	> 2.0 mm	< 2.0	> 2.0	
9. left max. stylet with many spines	present	absent	present	
10. max lever	present	absent	present	
11. pharynx rod	absent	present	absent	
12. number of pharynx tendons	> 14	± 10	> 14	
13. incision of salivary pump	present	absent	present	
14. adult scent-gland	1 reservoir 1 ostiole (excl. *Aepophilus)*	4 reservoirs 1 ostiole	2 reservoirs 2 ostioles	1 reservoir 2 ostioles
15. internal laterotergites	present	absent	absent	
16. coupling apparatus ♂	clothes-peg type	paper-clips type	absent	
17. abdominal spiracles	ventral	dorsal	dorsal	
18. pregenital glands	present (excl. *Aepophilus)*	absent	absent	absent
19. accessory canal ♀	absent	present	absent	present
20. spermathecal flange	mostly present	absent	present	absent
21. ovipositor	laciniate	plate-shape	intermediate	intermediate
22. parandria ♂	rigid	flexible	absent	absent
23. phallotheca	sclerotic	membranous	sclerotic	membranous
24. d. seminis-endosoma complex	contracted	long	long	long
25. endosomal sclerites	present	absent	present	absent
26. connection lig. processus-phallotheca	present	absent	absent	present
27. sclerotic strips in basal aula wall	absent	present	absent	absent

summarized in Table II. The gap between Saldidae and Leptopodidae amounts to 12 of the 27 characters selected and it has never been a point in the past to doubt the familial rank of both these groups. It is striking that each of the 27 characters used exclude *Omania-Corallocoris* from Saldidae, whereas both genera share 8 characters with Leptopodidae. Comparisons with Leotichiidae are not yet adequate, since anatomical and ontogenetic evidences are lacking.

I formally propose here to eliminate the genera *Omania* and *Corallocoris* from the Saldidae and to transfer them into a separate family, which must be named: *Omaniidae* stat. nov.

The four species of Omaniidae known at present, have a saldid-like rather than leptopodid or leotichiid facies. This is due to external features listed by China (1933) as

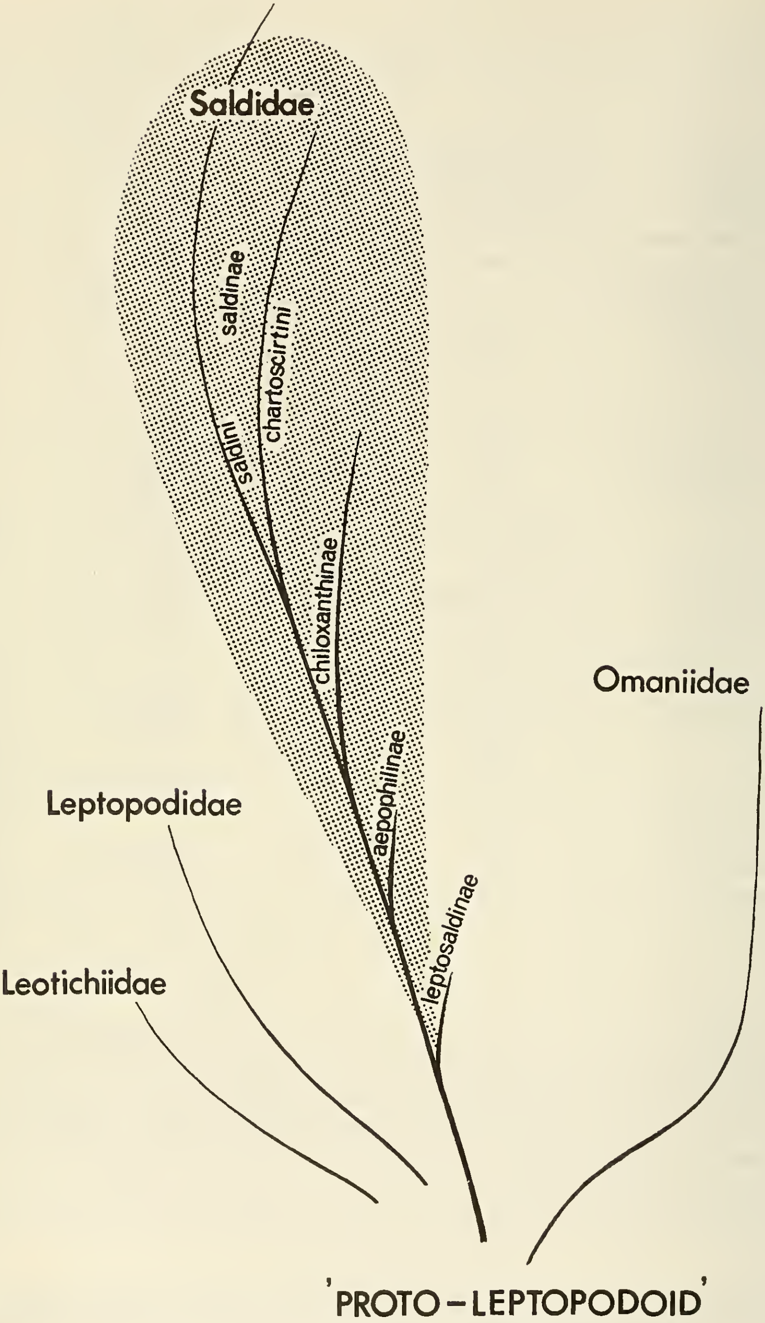

Fig. 13. Evolutionary diagram of Leptopodoidea

saldid characteristics: head inserted (v. exserted in Leptop. and Leot.); eyes not subpedunculate (v. subpedunculate); ocelli not upon prominently elevated tubercle (v. at top of elevation); rostrum extending beyond anterior coxae (v. shorter); posterior margin of pronotum straight or concave, surface not punctate (v. convex, strongly punctate); anterior femur and tibia normal (v. raptorial).

Many of the properties studied are liable to progressive evolution resulting in parallel development in different phyletic lines. Male genital structures, clasping organ, adult scent apparatus and, in particular, the chaetotaxy show distinct divergence from the usual leptopodoid patterns. In these respects, the Omaniidae represent a cladistically remote lineage; this is expressed with the more distant common origin in the evolutionary diagram (Fig. 13).

One may wonder why *Aepophilus* is not considered as belonging to a separate family. For, regarding the structures surveyed in the foregoing, this monobasic genus has often been mentioned as aberrant in Saldidae. The majority of the distinguishing characters of *Aepophilus,* however, fall within the ancestral-descendant range of the saldid lineage.

Therefore, its subfamily rank which I proposed in 1959 is here upheld, as it represents the most primitive living member of the family. A recently discovered fossil saldid from Mexico amber must be placed on an even lower level in a new subfamily: Leptosaldinae (Fig. 13), which will be described elsewhere (Cobben, in press).

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